The Molluscan Fauna of the Wawa River Region, Miskito Coast, Nicaragua: Ecology, Biogeographical Implications, and Descriptions of New Taxa

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ABSTRACT

Faunal surveys (1991–1992) of the biologically-unexplored Wawa River region of the Miskito Coast of Nicaragua have shown that the intertidal and estuarine areas contain four distinct molluscan assemblages; the *Neritina—Polymesoda* Assemblage, the *Littorina—Petricola* Assemblage, the *Agaronia-Micromactra* Assemblage, and the *Hastula—Donax* Assemblage, and that the shallow subtidal area contains a single assemblage, the *Ficus-Pacipecten* Assemblage. A list of macromollusks found in these five assemblages is given, and eight new endemic mollusks are described. These include: (Gastropods) *Ficus villai* n.sp. (Ficidae), *Cancellaria mediamericana* n.sp. (Cancellariidae), *Conus paschalli* n.sp. (Conidae), and (Bivalves) *Noetia* (s.s.) *lindae* n.sp. (Arcidae), *Plicatula miskito* n.sp. (Plicatulidae), *Mactra inceri* n.sp., *Micromactra miskito* n.sp. (both Mactridae), and *Petricola (Petricolaria) donnae* n.sp. (Petricolidae). This new faunal data, in conjunction with previous Central American biogeographical studies, has demonstrated the existence of a new molluscan faunal area within the western Caribbean, here referred to as "Miskitia". The Miskitian area, which may represent a new subprovince of the Caribbean Molluscan Province, is distinctly Panamic-appearing, containing molluscan assemblages that are dominated by normally-Eastern Pacific genera such as *Agaronia*, *Noetia* (s.s.), *Pacipecten*, and *Micromactra*

INTRODUCTION

Within the past decade, faunal surveys in previously-unexplored areas of the Caribbean Sea region have uncovered large numbers of new and unusual marine mollusks (Petuch, 1987, 1988, 1990). Besides underscoring our lack of knowledge of such geographically-proximate malacofaunas, these discoveries have shown that the Caribbean is not faunally homogeneous as was previously thought (Warmke & Abbott, 1961), but is composed of at least seven discrete, mutually-exclusive subregions (Petuch, 1981,1982,1987,1988, 1997). Each of these subregions has been found to contain a high degree of endemism at both the generic and specific level and, altogether, have demonstrated that the geographically-small Caribbean Sea region contains the highest level of molluscan diversity found in the Americas.

While the coastal faunas of the Yucatan Peninsula, Honduras (Petuch, 1981,1987,1988; Vokes & Vokes, 1983), Costa Rica (Houbrick, 1968), and Panama (Olsson & McGinty, 1958; Petuch, 1990; Radwin, 1969) have been studied, the mollusks of the Caribbean coast of Nicaragua had never been adequately surveyed and the region has remained enigmatic. Over the past ninety years, only a few scattered reports on Caribbean Nicaraguan mollusks have appeared in the literature (reviewed in next section), and these have only offered tantalizing bits of information that hinted at a very unusual and highly endemic fauna. In December, 1991 and July, 1992, while working with the Caribbean Conservation Corporation of Gainesville, Florida (under the auspices of IRENA (Instituto de Recursos Naturales), the environmental agency of the Nicaraguan government), I had the opportunity to visit and collect along a part of the Miskito Coast near the mouth of the Wawa River. This study, coincidentally conducted in the only area of the entire coast that had ever been sampled (Fluck, 1905a, 1905b, 1905c, 1905d, 1905e, 1906; see next section), is part of a major biotic survey that is being undertaken by the Nicaraguan government in preparation of the establishment of a wildlife and cultural protected zone along the Miskito Coast.

The Miskito Coast was found to contain a highly unusual molluscan fauna, one that was both atypical of the Caribbean Molluscan Province and that exhibited a high degree of endemism. In many ways, the Nicaraguan Caribbean coastal malacofauna more closely resembles the faunas of the Eastern Pacific Panamic Province and the eastern South American Brazilian Province than it does

the fauna of the surrounding Caribbean Province. This Panamic-Brazilian appearance was further emphasized by the discovery of new endemic species, several of which belong to genera that were thought to have been restricted to the Panamic and Brazilian Provinces.

In this paper, descriptions of the various coastal environments of the Wawa River area are given, along with lists of the dominant macromollusks found in each habitat. Eight new Miskito Coast species are described, including: Gastropods—*Ficus villai* n.sp. (Ficidae), *Cancellaria mediamericana* n.sp. (Cancellariidae), *Conus paschalli* n.sp. (Conidae); Bivalves—*Noetia lindae* n.sp. (Arcidae), *Plicatula miskito* n.sp. (Plicatulidae), *Mactra inceri* n.sp., *Micromactra miskito* n.sp. (both Mactridae), and *Petricola (Petricolaria) donnae* n.sp. (Petricolidae). A discussion of the biogeographical relationships of the Miskito Coast fauna is given in the final section.

Previous Malacological Research Along The Miskito Coast Of Nicaragua

Prior to the present research, only one other attempt at a comprehensive survey of the macromollusks of the Miskito Coast had ever been undertaken. This pioneer work was done by the Rev. W.H. Fluck, a Moravian missionary who ministered to the Miskito and Sumo Indians at the turn of the century. In a series of six papers published in 1905 and 1906, Fluck gave interesting anecdotal insights into the environments and natural history of the area, molluscan food utilization by the local Indians, and detailed descriptions of some of his techniques for collecting mollusks. Most importantly, he provided several annotated species lists, arranged phylogenetically, of the gastropods and bivalves that had been collected near the mouth of the Wawa River, Wounta and Bluefields Lagoons, and the offshore Man-of-War and King's Keys.

In four of his papers, Fluck lists fifty-two species of marine and estuarine mollusks from the Wawa River area, one of which he described as new (*Strombus pugilis nicaraguensis* Fluck, 1905). Of these, five were not encountered in the present study; the gastropods *Tonna maculosa, Polinices lacteus, Cymatium pileare*, and *Columbella mercatoria*, and the bivalve *Arcopagia fausta*. Here, arranged by publication date, are lists of Fluck's Wawa species, along with their updated taxonomic designations (where applicable);

Fluck, 1905b. (*Shell Collecting on the Mosquito Coast of Nicaragua—II.* The Nautilus 19(2):16–19).

Fluck's Taxon	Updated Nomenclature
Murex brevifrons Lamarck	*Chicoreus mergus* E. Vokes
Murex bellus Reeve	*Vokesimurex garciai* (Petuch)
Cymatium pileare Lamarck	
Purpura floridana Conrad	*Thais floridana* (Conrad)
Fasciolaria tulipa Linnaeus	
Melongena melongena Linnaeus	
Nassa vibex Say	*Nassarius vibex* (Say)
Voluta virescens Solander	*Voluta lacertina* Petuch
Marginella apicina Menke	*Prunum pruinosum* (Hmds)
Marginella guttata Dillwyn	*Prunum guttatum* (Dillwyn)
Oliva(Agaronia) testacea Lam.	*Agaronia hilli* Petuch
Columbella mercatoria Linnaeus	
Columbella (Anachis) lyrata Sow	*Costanachis veleda* (Duclos)
Cancellaria reticulata Linnaeus	*Cancellaria mediamericana* n.sp.
Terebra cinerea Gmelin	*Hastula cinerea* (Born)

Fluck, 1905d (*Shell Collecting on the Mosquito Coast of Nicaragua—IV.* The Nautilus 19(5):55–57).

Fluck's Taxon	Updated Nomenclature
Cypraea exanthema Linneaus	*Cypraea zebra* Linnaeus
Dolium perdix Linnaeus	*Tonna maculosa* Linnaeus
Pyrula papyratia Say	*Ficus villai* n.sp.
Polinices brunnea Link	*Polinices hepaticus* (Röding)
Polinices lacteus Guilding	
Crepidula convexa Say	
Vermicularia spirata Philippi	
Litorina lineata Philippi	*Littorina lineata* d'Orbigny
Litorina columellaris D'Orb.	*Littorina nebulosa* (Lamarck)
Litorina angulifera Lam.	*Littorina angulifera* (Lamarck)
Neritina lineata var. *reticulata*	*Neritina piratica* Russell, 1940

Fluck, 1905e. (*Shell Collecting on the Mosquito Coast of Nicaragua-V.* The Nautilus 19(7):78–80).

Fluck's Taxon	Updated Nomenclature
Pholas campechiensis Gmelin	
Tagelus pocyii Dall	*Tagelus plebeius* (Lightfoot)
Periploma inequivalvis Schum.	*Periploma margaritaceum* (Lamarck)
Mactra(Mactrella) alata Spengler	*Mactrellona alata* (Spengler)
Mulinia guadeloupensis Recluz	*Mulinia cleryana* (Orbigny)

Fluck, 1906. (*Shell Collecting on the Mosquito Coast of Nicaragua-VI.* The Nautilus 20(1):1–4).

Fluck's Taxon	Updated Nomenclature
Tellina (Eurytellina) angulosa Gmelin	
Tellina (Cyclotellina) fausta Pulteney	*Arcopagia fausta* (Pulteney)
Sanguinolaria (Psammotella) operculata(Gmelin)	*Sanquinolaria cruenta* (Lightfoot)
Strigilla carnaria Linnaeus	
Iphigenia brasiliana (Lamarck)	
Donax denticulatus Linnaeus	
Donax cayennensis Lamarck	*Donax striatus* Linnaeus
Pitar (Hysteroconcha) dione (Linnaeus)	
Chione cancellata (Linnaeus)	
Cyrena (Polymesoda) panamensis Prime	*Polymesoda placans (Hanley)*

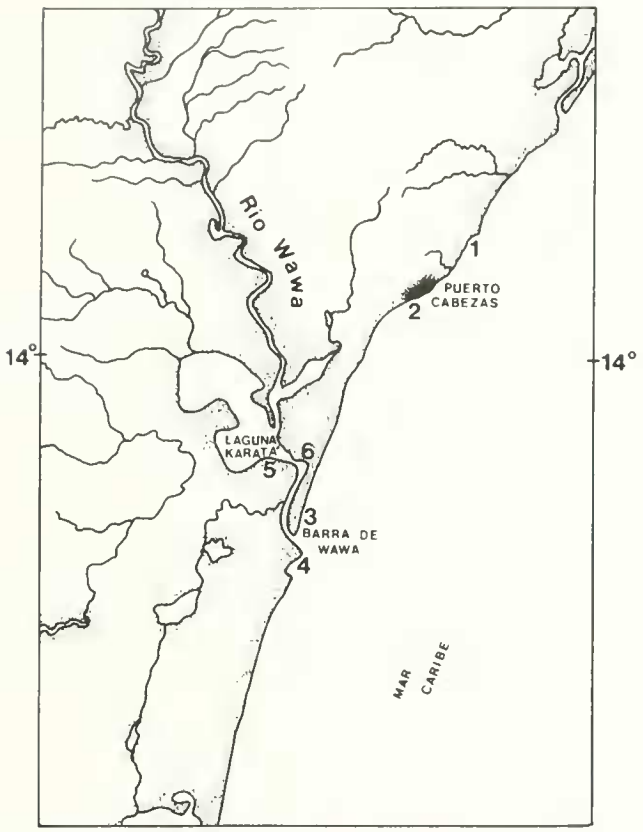


Figure 1. Map of the Miskito Coast of Nicaragua, in the vicinity of the Wawa River mouth, showing collection stations. Distance between Stations 1 and 4 is approximately 11 km. 1 = shallow embayment on southern side of Bragman's Bluff (containing *Agaronia—Micromactra* Assemblage); 2 = clay cliffs and clay talus "reefs" immediately north and south of Puerto Cabezas (containing *Littorina—Petricola* Assemblage); 3 = beach on outer side of Barra de Wawa, northern side of Wawa River mouth (containing *Hastula—Donax* and *Ficus—Pacipecten* Assemblages); 4 = beach on southern side of Wawa River mouth, adjacent to Wawa Village (containing *Hastula—Donax* and *Ficus—Pacipecten* Assemblages); 5 = southern shore of Laguna Karatá, at Karatá Village (containing *Neritina—Polymesoda* Assemblage); 6 = mangrove jungle at Salonque de Kauropura (containing *Neritina—Polymesoda* Assemblage).

Tivela mactroides (Born)	
Chama congregata Conrad	
Arca umbonata Lamarck	*Arca imbricata* Bruguière
Scapharca incongrua var. *brasiliana* Lam.	*Anadara brasiliana* (Lamarck)
Arca occidentalis Philippi	*Arca zebra* (Swainson)
Pinna muricata Linnaeus	*Atrina seminuda* (Lamarck)
Pecten dislocatus Say	*Pacipecten leucophaeus* (Reeve)
Ostrea virginica Gmelin	*Crassostrea virginica* (Gmelin)

Since Fluck's series of papers, only a few scattered references to the Miskito Coast fauna have appeared in the Caribbean molluscan literature. Most of these have been in the *Johnsonia* series of monographs published at Harvard University (1941–1974)(ie. Clench & Abbott, 1941; Bequaert, 1942, *etc.*), and were based upon the Fluck Collection in the Museum of Comparative Zoology. No references to newly-collected Miskito material have been mentioned prior to the present study.

In the 1980's, I had received several suites of unusual western Caribbean gastropods from local commercial shell dealers, particularly Mr. Leonard C. Hill of Miami, Florida. Within these specimen lots were large numbers of new species that had been dredged from shallow depths (10–35m) off Roatan Island and the northern Honduras coast by commercial shrimp boats. Many of these were subsequently described by myself (Petuch, 1987) and were later discussed within a geochronological and biogeographical framework (Petuch, 1988:149–156). Although the bulk of these new taxa were from the area immediately north of the Miskito Coast, a few have now been collected in Nicaragua and have been found to be ecologically-dominant Miskito organisms. Two of these recently described gastropods, which range from the Roatan Island-Punta Patuca area of Honduras to the Nicaraguan Miskito Coast, include *Agaronia hilli* Petuch, 1987 and *Vokesimurex garciai* (Petuch, 1987).

Following the legacy of the Rev. Fluck and his pioneer research, I here report on the most recent malacological survey of the Miskito Coast. In total, one hundred and four species, from five distinct molluscan assemblages, were collected, doubling Fluck's total of fifty-two species. Of these, eight are new to science. The habitats and ecological preferences of the molluscan assemblages of the Wawa River area of the Miskito Coast are given in the following section.

Collecting Stations And Coastal Environments

In order to gain a general insight into the molluscan faunas of the varied coastal habitats, six widely-spaced collecting sites were selected in the Puerto Cabezas-Wawa River area (Figure 1). Four of these were along the open coast, ranging from approximately 2.5 km north of the main pier of Puerto Cabezas southward to the southern shore of the Wawa River mouth. Two others were from within the estuary of the Wawa River. From these six sites, altogether, five distinct molluscan assemblages could be discerned. The assemblages are named after dominant or characteristic gastropods and bivalves, one of each, and these include: *1.* The *Neritina—Polymesoda* Assemblage (brackish water, estuarine), 2. the *Littorina—Petricola* Assemblage (coastal clay cliffs), 3. the *Agaronia—Micromactra* Assemblage (protected coastal, quiet intertidal), *4.* the *Hastula—Donax* Assemblage (open coastal, high energy intertidal), and 5. the *Ficus—Pacipecten* Assemblage (offshore, shallow subtidal). The physical environment and molluscan assemblages of each collecting site are discussed herein.

Station 1. (*Agaronia—Micromactra* Assemblage)

An unnamed, widely open embayment containing shallow, relatively quiet water conditions, was located at ap-

proximately 2.5 km north of Puerto Cabezas, between the mouth of La Bocana Creek and Bragman's Bluff. The southward curvature of Bragman's Bluff, along with its accompanying sandstone and clay block talus reef, both offer protection from strong easterly and northeasterly winds and waves, allowing the creation of almost lagoonal conditions within the open embayment. These quiet conditions, which are especially prevalent immediately south of the bluff, are further enhanced by the presence of a large sand bar that runs parallel to the coast just offshore.

This shallow (0–1m depth) environment, comprising a flat muddy-sand substrate and murky water conditions with only minimal wave action, contained a highly unusual, highly atypical Caribbean molluscan assemblage. The dominant mollusks, found nowhere else in the Caribbean province, give this assemblage a distinctive Eastern Pacific appearance, and the entire community closely resembles assemblages that are found on similar biotopes along western Central America. Characteristic mollusks from the Bragman's Bluff open embayment locality include:

Gastropods

Strombus pugilis nicaraguensis Fluck, 1905 (Figure 6)
Agaronia hilli Petuch, 1987 (Figures 4, 5)
Conus paschalli n.sp. (Figures 2,3)

Bivalves

Noetia lindae n.sp. (Figures 9, 10)
Plicatula miskito n.sp. (Figures 16–19)
Diplodonta notata (Dall & Simpson, 1901)
Trachycardium muricatum (Linnaeus, 1758)
Mactra inceri n.sp. (Figures 7, 8, 11)
Micromactra miskito n. sp. (Figures 12, 13)
Mulinia cleryana (Orbigny, 1846) (Figure 20)
Macoma brevifrons (Say, 1834)
Macoma constricta (Bruguière, 1792)
Tellina punicea Born, 1778
Sanguinolaria sanguinolenta (Gmelin, 1791)
Periploma margaritaceum (Lamarck, 1801) (Figure 21)

Similar biotopes from around the Caribbean Basin all contain assemblages that are typically dominated by olivid gastropods of the genera *Oliva* (particularly members of the *Oliva reticularis* Lamarck, 1811 species complex; see Petuch & Sargent, 1986:120–122) and *Olivella*, and bivalves of the genera *Glycymeris*, *Divaricella*, *Codakia*, *Anomalocardia*, and the tellinids *Tellina radiata* Linnaeus, 1758 and *Tellina listeri* Röding, 1798. All of these taxa were missing from the Bragman's Bluff collecting station and were not found at any other Miskito coast locality (both this study and that of the Rev. Fluck in 1905–1906). Instead, the gastropod component at Bragman's Bluff was dominated by the olivid genus *Agaronia* and the bivalve component by mactrids (*Mactra*, *Micromactra*, and *Mulinia*). The primarily-Panamic genus *Micromactra* (represented by *M.miskito* n.sp.), previously unknown in the Caribbean Province, was especially common at Station 1.

Behind the sand bar, directly off the beach south of Bragman's Bluff, large beds of dead bivalve shells have accumulated. These beds, composed mostly of dead *Noetia* valves, produce the proper substrate for the attachment of the dwarf oyster, *Plicatula miskito* n.sp.. This new species, which closely resembles the Eastern Pacific *Plicatula penicillata* Carpenter, 1857, further demonstrates the Panamic appearance of the Bragman's Bluff assemblage.

Station 2. (*Littorina—Petricola* Assemblage)

From the main pier of Puerto Cabezas northward to the mouth of Laguna Krukira (approximately 8 km north), the coast is characterized by high (20–50m) red and white clay cliffs (Figure 14). Lenses of rounded quartzite pebbles are plentiful within the cliffs and, upon erosion, often form thick pebble beds at the cliff bases. At several localities immediately north of the pier, and particularly adjacent to the mouth of La Bocana Creek, large talus slopes composed of massive blocks of clay and soft sandstone have extended seaward and have, in effect, produced "rocky" intertidal environments. These clay "reefs" often extend into the subtidal region and offer a wide variety of habitats within the vertical range. The clay cliffs biotope at, and immediately northward of Puerto Cabezas, was chosen as the second collection station.

The intertidal-shallow subtidal clay cliff and clay "reef" environment contained a very impoverished molluscan fauna, with only a few species dominating the area. Characteristic mollusks from the Puerto Cabezas clay cliffs locality include:

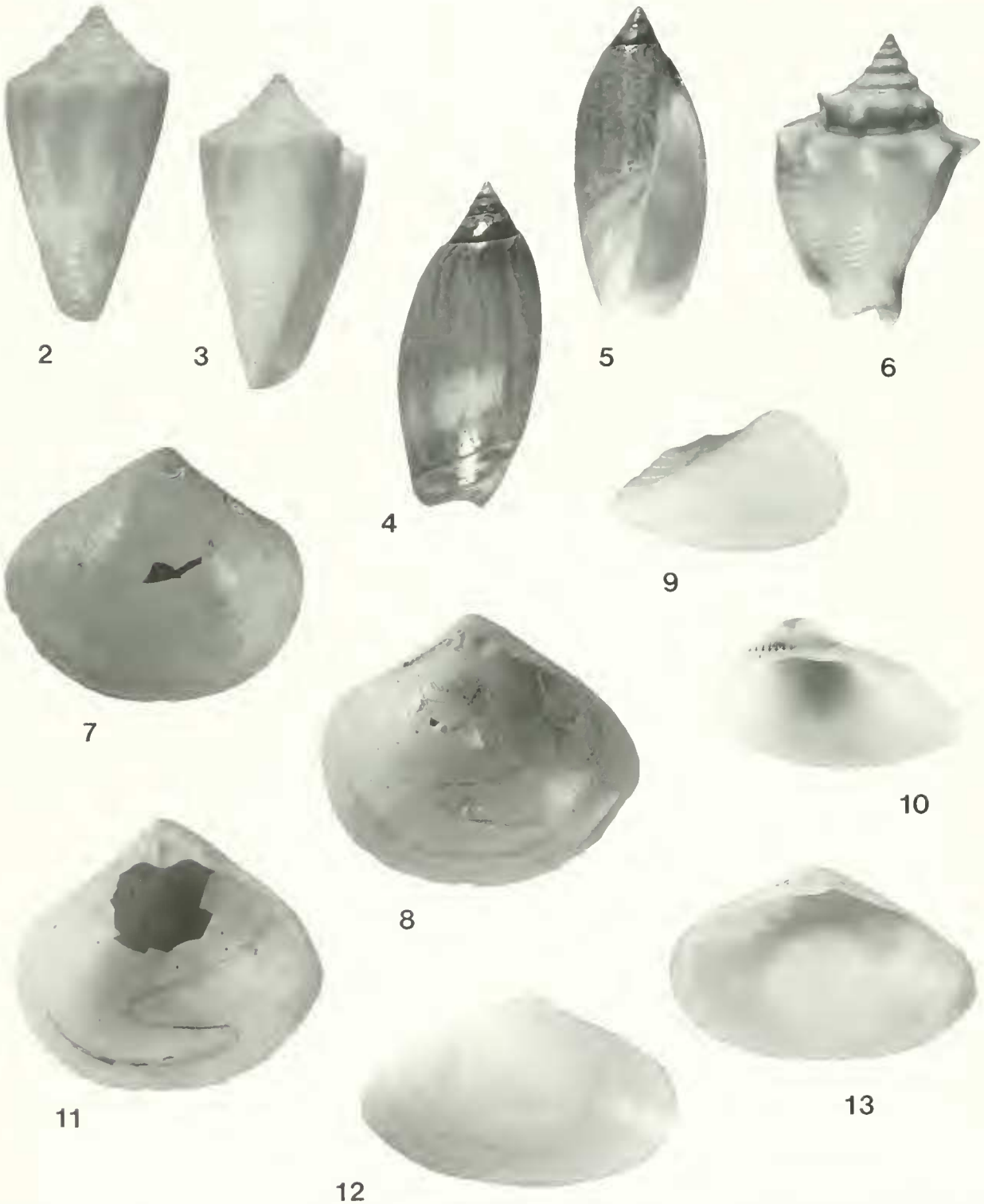
Gastropods

Diodora cayenensis (Lamarck, 1822)
Littorina lineata Orbigny, 1842
Littorina nebulosa (Lamarck, 1822)
Littorina riisei Mörch, 1876
Thais floridana (Conrad, 1837)

Bivalves

Pholas campechiensis Gmelin, 1791
Petricola (Petricolaria) donnae n.sp. (Figures 24, 25)

What was particularly impressive about the clay cliffs fauna was the noticeable absence of typical common Caribbean hard substrate taxa, many of which were expected to have been encountered along this coast. Absent from the supratidal zone were the classically Caribbean littorinid genera *Tectarius (Cenchritis)*, *Nodilittorina (Echinolittorina)* and *Echininus*. Within the intertidal zone, the absence of the neritid genera *Linnerita*, *Theliostyla*, and *Puperita*, the potamidid genus *Batillaria*, the cerithiid genus *Cerithium (Thericium)*, and the pulmonate genus *Siphonaria* was particularly



Figures 2–13. Mollusks characteristic of the *Agaronia*—*Micromactra* Assemblage. **2, 3.** *Conus* (*Leptoconus*) *paschalli* new species, holotype, length 26 mm; **4, 5.** *Agaronia hilli* Petuch, 1987, length 39 mm; **6.** *Strombus pugilis nicaraguensis* Fluck, 1905, length 58 mm; **7, 8.** *Mactra inceri* new species, holotype, length 35.5 mm; **9, 10** *Noetia* (s.s.) *lindae* new species, holotype, length 25.5 mm; **11.** *Mactra inceri* new species, paratype, length 34 mm (pallial line outlined with ink); **12, 13.** *Micromactra miskito* new species, holotype length 30 mm.

Figure 14. Aerial view of clay cliff coastline in the vicinity of Puerto Cabezas. Arrows point to clay talus "reefs" near the mouth of La Bocana Creek, on the northern side of the city. Station 2 included these cliffs and "reefs" and others immediately to the south (to the left). The holotype of *Petricola (Petricolaria) donnae* n.sp. was collected on the beach between the first two arrows on the left.

noteworthy. Instead, the entire intertidal zone was dominated by only three species of *Littorina*, of which *Littorina nebulosa* (Lamarck, 1822) was the most abundant.

The shallow subtidal zone of the clay "reefs" exposed at extreme low tides, was relatively barren externally, but was riddled with immense numbers of holes. The holes represented the burrows of the pholadid and petricolid bivalves *Pholas campechiensis* Gmelin, 1791 and *Petricola (Petricolaria) donnae* n.sp., and these two burrowers were the dominant organisms in this area. The large carnivorous muricoidean gastropod *Thais floridana* (Conrad, 1837) was also frequently encountered on the subtidal clay "reefs", and several specimens were found to be feeding on the limpet *Diodora cayenensis* (Lamarck, 1822).

Stations 3 and 4. (*Hastula—Donax* Assemblage and *Ficus—Pacipecten* Assemblage).

South of the Puerto Cabezas pier, the high clay cliffs disappear, and the coastline becomes flattened with wide, jungle-lined beaches and high-energy surf zones. Along these beaches two distinct molluscan assemblages accumulate; a *Hastula-Donax*-dominated assemblage that lives in the sandy intertidal zone amid the heavy surf, and a *Pacipecten* dominated assemblage that lives in the subtidal area directly offshore (approximately 0.5 to 1 km off the coast, in depths of 10–25m). Most of the components of the former assemblage can be collected within the surf at low tide and their dead, beached shells are unusually well-preserved. The components of the latter assemblage, on the other hand, only wash up onto the beach after storms or heavy blows, and their shells are most always in a smashed, fragmentary condition. Preliminary information on the composition of Caribbean beach communities (ie. Warmke & Abbott, 1961: 17,19; Houbrick, 1968) and western Caribbean offshore communities (Radwin, 1969:229–236; Petuch, 1987:62–63; Petuch, 1990) made it possible to determine which of the two assemblages represented the home communities of all beach specimens collected.

The high-energy beach environment, the biotope of the *Hastula-Donax* Assemblage, houses the most typical Caribbean fauna found along the Miskito Coast. For study, two beach areas that particularly characterized this biotope were selected on either side of the Wawa River mouth; with Station 3 located on the northern side along the outer coast of the Barra de Wawa, and with

Figure 15. View of the beach along the southern side of the Wawa River mouth. Piles of driftwood, brought down by the strong river currents, line the beach for several kilometers. The Fig Shell, *Ficus villai* n.sp., and the scallop, *Pacipecten leucophaeus* (Reeve, 1852), were especially common along this area. Station 4 included this locality and the open beach environment in the distance. This is also the type locality of Fluck's *Strombus pugilis nicaraguensis* (which is plentiful as fresh beach specimens).

Station 4 located on the southern side adjacent to Wawa Village (Figure 15). Characteristic mollusks from the Wawa surf locality include:

Gastropods

Hastula cinerea (Born, 1778)

Bivalves

Solen obliquus Spengler, 1794
Strigilla carnaria (Linnaeus, 1758)
Strigilla gabbi Olsson and McGinty, 1958
Strigilla mirabilis (Philippi, 1841)
Strigilla pisiformis (Linnaeus, 1758)
Strigilla producta (Tryon, 1870)
Strigilla pseudocarnaria Boss, 1969
Tellina sybaritica Dall, 1881
Donax denticulatus Linnaeus, 1758
Donax mediamericanus Pilsbry, 1919 (Figure 43)
Donax striatus Linnaeus, 1767 (Figure 42)
Iphigenia brasiliana (Lamarck, 1818)
Tagelus plebeius (Lightfoot, 1786)
Pitar dione (Linnaeus, 1758)
Tivela mactroides (Born, 1778)

With the exception of *Donax mediamericanus* Pilsbry, 1919, which is endemic to the Caribbean coast of Central America (type locality, Livingston, Guatemala), all of the other members of this assemblage are wide-ranging tropical western Atlantic surf-loving species. Although the faunal composition of this assemblage is, by itself, unremarkable, the abundant presence of six sympatric species of the tellinid genus *Strigilla* and three species of large *Donax* is noteworthy. Other Caribbean surf eco-

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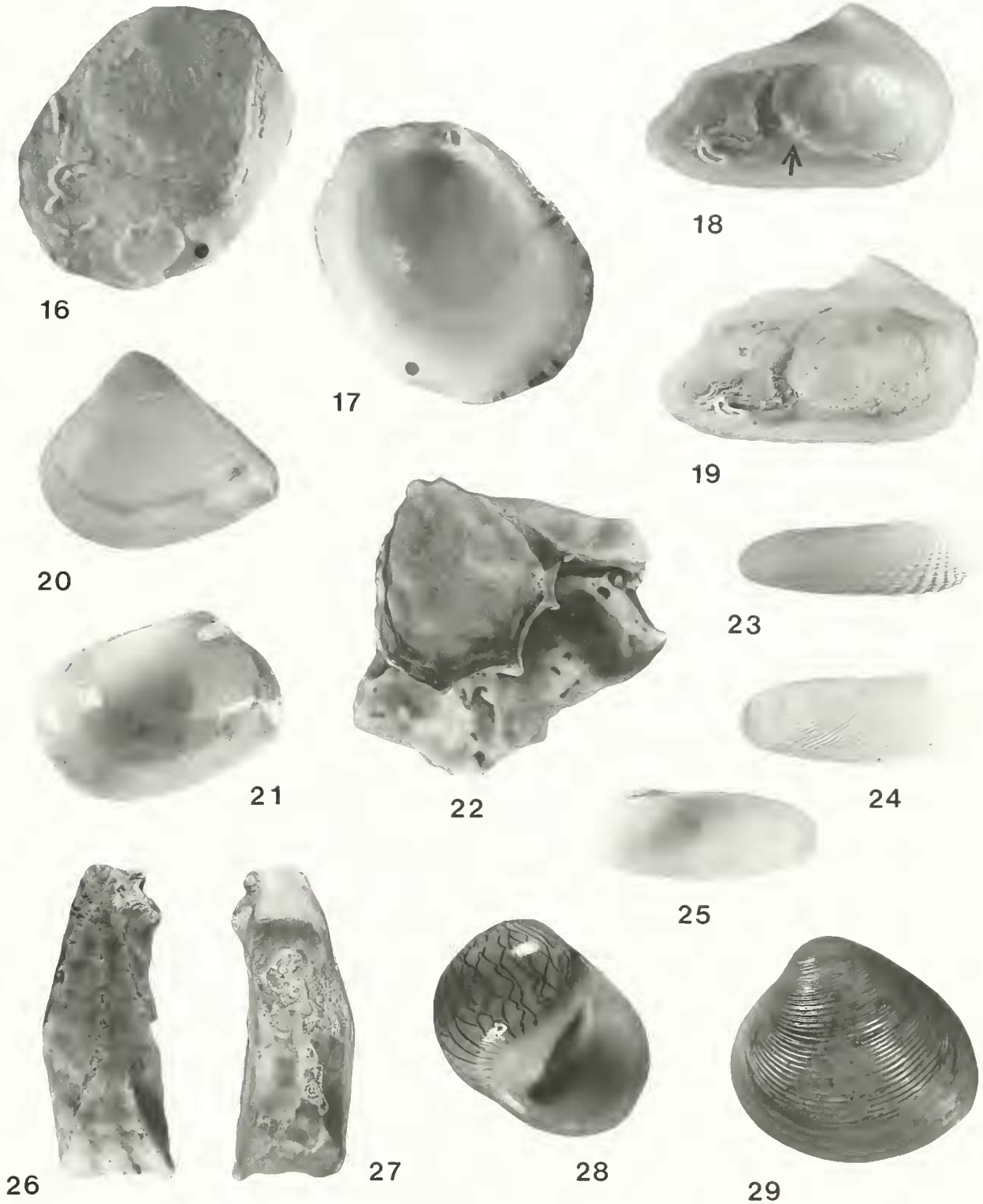
Figure 16–29. Mollusks characteristic of the *Agaronia—Micromactra, Littorina—Petricola,* and *Neritina—Polymesoda* Assemblages. **16, 17.** *Plicatula miskito* new species, upper valve of holotype, length 13 mm; **18.** *Plicatula miskito* new species, interior view of bottom valve of holotype attached to interior of *Noetia lindae* valve. Arrow points to spondyloid hinge; **19.** *Plicatula miskito* new species, upper valve of holotype attached to bottom valve in life position, within *Noetia lindae* valve; **20.** *Mulinia cleryana*



(d'Orbigny, 1846), length 23 mm; **21.** *Periploma margaritaeeum* (Lamarck, 1801), interior of left valve, length 31 mm; **22.** *Crassostrea rhizophorae* (Guilding, 1828) upper specimen length 35 mm; **23.** *Petricola (Petricolaria) pholadiformis* (Lamarck, 1818), length 35 mm. From beach at Lake Worth, Florida, (for comparison with *Petricola donnae*); **24, 25.** *Petricola (Petricolaria) donnae* new species, holotype, length 28 mm; **26, 27.** *Crassostrea virginica* (Gmelin, 1791), length 97 mm. Elongated variant that resembles *Crassostrea labelleensis* Olsson & Harbison, 1953 from the Floridian Pleistocene; **28.** *Neritina piratica* Russel, 1940, length 13 mm; **29.** *Polymesoda placans* (Hanley, 1845), length 28 mm.

Figure 30. View of a section of the red mangrove (*Rhizophora mangle*) forest at Salonque de Kanropura, near Laguna Karatá. The arrow (extreme lower left center) points to a small clump of the mangrove oyster, *Crassostrea rhizophorae* (Guilding, 1828). The nerites *Neritina piratica* Russell, 1940 and *Neritina reclivata* (Say, 1822) were common here on submerged roots and oyster clumps. On the higher dry branches and roots, the periwinkles *Littorina nebulosa* (Lamarck, 1822) and *Littorina angulifera* (Lamarck, 1822) and the melampid *Melampus coffeus* (Linnaeus, 1758) could be found in abundance. Open muddy-sand bottom areas between mangrove forests housed large, dense colonies of the corbiculid bivalve *Polymesoda placans* (Hanley, 1845). This area encompassed Station 6.

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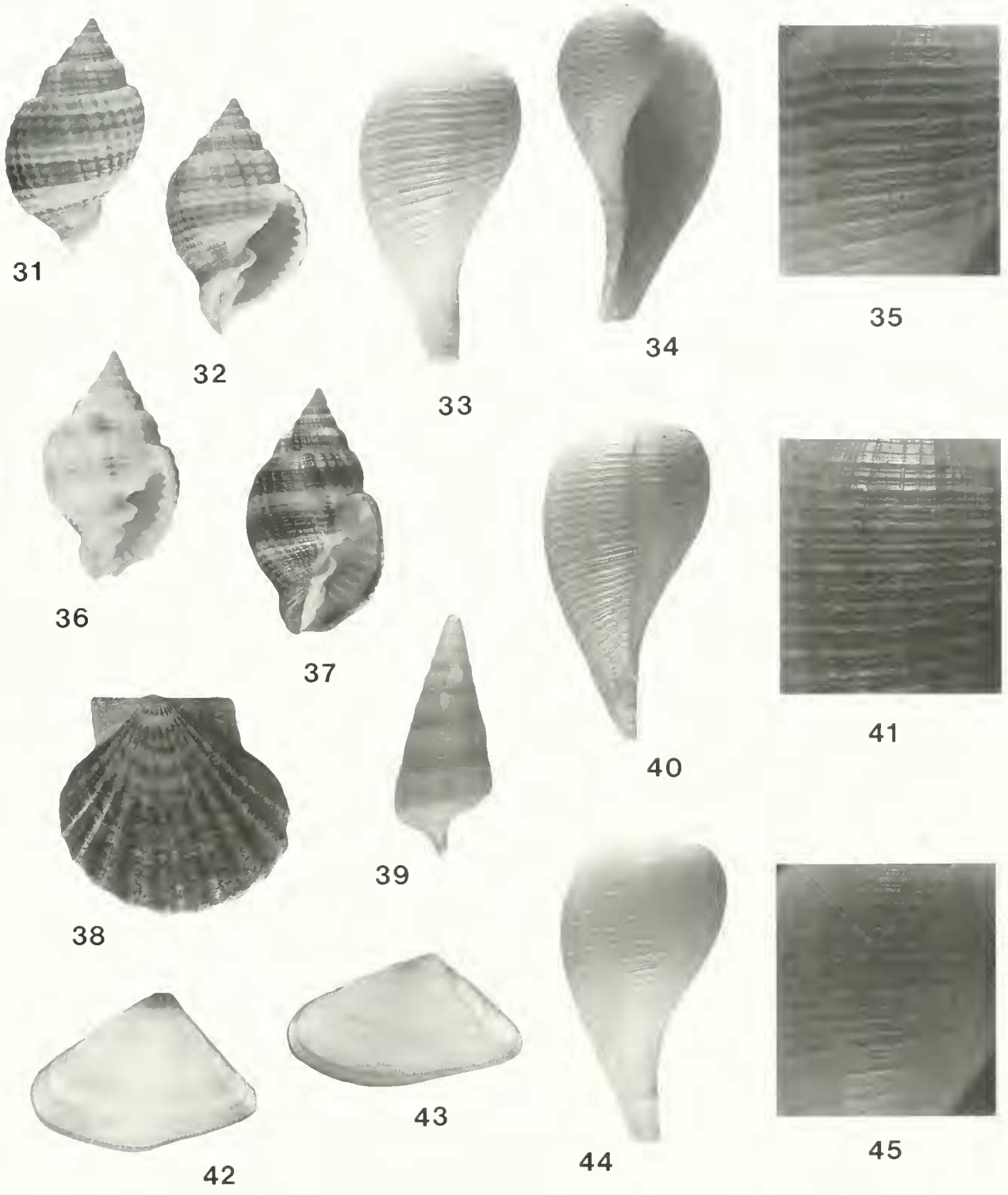
Figures 31–45. Mollusks characteristic of the *Ficus—Pacipecten* and *Hastula—Donax* Assemblages. **31, 32.** *Cancellaria mediamericana* new species, holotype, length 34 mm, **33, 34.** *Ficus villai* new species, holotype, length 67 mm, **35.** Detail of shell sculpture of holotype of *Ficus villai*; **36.** *Cancellaria reticulata* (Linnaeus, 1767), length 27 mm. From beach at Sanibel Is., Florida.



for comparison with *Cancellaria mediamericana*; **37.** *Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992, length 35 mm. Trawled from 25 m depth off Victoria, Espirito Santo, Brazil. for comparison with *Cancellaria mediamericana*; **38.** *Pacipecten leucophaeus* (Reeve, 1852), length 38.5 mm; **39.** *Cerithioclava garciai* Houbrick, 1985, juvenile specimen, length 34 mm; **40.** *Ficus lindae* Petuch, 1988, length 99 mm.Trawled from 20 m depth off the Monges Islands, Gulf of Venezuela, for comparison with *Ficus villai*; **41.** Detail of shell sculpture of *Ficus lindae*; **42.** *Donax striatus* Linnaeus, 1767, length 34 mm; **43.** *Donax mediamericanus* Pilsbry, 1919, length 30 mm; **44.** *Ficus communis* Röding, 1798, length 67 mm. From beach at Sanibel Is., Florida, for comparison with *Ficus villai*; **45.** Detail of shell sculpture of *Ficus communis*.

systems usually contain one or two *Donax* species and only two or three *Strigilla* species.

The other molluscan assemblage found along the Wawa beaches, the *Ficus-Pacipecten* Assemblage, is probably only partially represented, with its community structure data being biased toward those species whose shells most readily accumulate along the shore after storms. Nevertheless, sufficient information exists about this intriguing and unstudied ecosystem, mostly gleaned from beach deposits, to show that this offshore community is, in many ways, as atypical of the Caribbean region as is the *Agaronia—Micromactra* Assemblage of shallower water areas. Characteristic mollusks of the Miskito Coast offshore, subtidal area include:

Gastropods

Turbo castanea Gmelin, 1791
Vermicularia spirata (Philippi, 1836)
Cerithioclava garciai Houbrick, 1985 (Figure 39)
Crepidula convexa Say, 1822
Xenophora conchyliophora (Born, 1780)
Cypraea (Macrocypraea) zebra Linnaeus, 1758
Pseudocyphoma intermedia (Sowerby, 1828)
Naticarius canrena (Linnaeus, 1758)
Polinices hepaticus (Röding, 1798)
Phalium granulatum (Born, 1778)
Distorsio robinsoni Petuch, 1987
Tonna galea (Linnaeus, 1758)
Ficus villai n.sp. (Figures 33, 34, 35)
Chicoreus brevifrons (Lamarck, 1822)
Chicoreus mergus (E.Vokes, 1974)
Vokesimurex cabrittii (Bernardi, 1859)
Vokesimurex garciai (Petuch, 1987)
Talityphis expansus (Sowerby, 1874)
Costanachis veleda (Duclos, 1846)
Nassarius vibex (Say, 1822)
Fasciolaria tulipa (Linnaeus, 1758)
Fusinus dowianus (Olsson, 1954)
Vasum muricatum (Born, 1778)
Voluta lacertina Petuch, 1990
Cancellaria mediamericana n.sp. (Figures 31, 32)
Prunum guttatum (Dillwyn, 1817)
Prunum pruinosum (Hinds, 1844)
Conus aureopunctatus Petuch, 1987
Conus daucus Hwass, 1792
Conus garciai daMotta, 1982
Conus rosemaryae Petuch, 1990
Conus spurius Gmelin, 1791
Terebra taurina Lightfoot, 1786

Bivalves

Arca imbricata Bruguière, 1789
Arca zebra (Swainson, 1833)
Anadara brasiliana (Lamarck, 1819)
Anadara ovalis (Bruguière, 1789)
Barbatia domingensis Lamarck, 1819
Caloosarca notabilis (Röding, 1798)
Atrina seminuda (Lamarck, 1819)
Argopecten gibbus (Linnaeus, 1758)
Pacipecten leucophaeus (Reeve, 1852) (Figure 38)
Lopha equestris Say, 1834
Diplodonta semiaspera (Philippi, 1836)
Chama congregata Conrad, 1833
Laevicardium laevigatum (Linnaeus, 1758)
Mactrellona alata (Spengler, 1802)
Tellina angulosa Gmelin, 1791
Tellina similis Sowerby, 1806
Sanguinolaria cruenta (Lightfoot, 1786)
Chione cancellata (Linnaeus, 1767)
Chione (Lirophora) latilirata (Conrad, 1841)
Chione (Lirophora) paphia (Linnaeus, 1767)
Pitar circinatus (Born, 1778)
Corbula contracta Say, 1822

Because of their thin and lightweight but yet structurally-strong shells, *Ficus villai* n.sp. and *Pacipecten leucophaeus* (Reeve, 1852) (single valves) are collected abundantly along the beach, most often in perfect condition. Judging from its abundance as beach shells, the western Caribbean endemic *Pacipecten leucophaeus* must form dense beds just offshore, much as the closely-related analogue species *Pacipecten tumbezensis* (d'Orbigny, 1846) does along the subtidal areas off western Central America. The Panamic appearance of the Miskito Coast subtidal assemblage is further enhanced by the presence of *Ficus villai* n.sp. (possibly a close relative of the Panamic *Ficus ventricosa* (Sowerby, 1825)) and by *Cancellaria mediamericana* n.sp. (resembling members of the Panamic *Cancellaria obesa* Sowerby, 1832 species complex). The subtidal assemblage also shows a close relationship to the faunas of Caribbean Honduras to the north (Petuch, 1987; Petuch, 1988:155–156) and to Caribbean Panama in the south (Petuch, 1990), especially in containing such distinctive western Caribbean endemics as *Cerithioclava garciai* Houbrick, 1985, *Vokesimurex garciai* (Petuch, 1987), *Fusinus dowianus* Olsson, 1954, *Voluta lacertina* Petuch, 1990, *Conus garciai* da Motta, 1982, *Conus rosemaryae* Petuch, 1990, and *Conus aureopunctatus* Petuch, 1987.

Stations 5 and 6. (*Neritina—Polymesoda* Assemblage)

The Wawa River and its numerous small tributaries expand into three large lagoons before coalescing and narrowing into a single large final channel. These lagoons, the Laguna Yulu-Laguna Karatá complex (to the west of the main Wawa channel) and the smaller Laguna Kauropura (to the east of the main channel) come together near the Salonque de Kauropura, producing a rechannelized Wawa River mouth that empties into the Caribbean Sea approximately 11 km south of Puerto Cabezas. The headwaters of these lagoons are essentially freshwater, becoming brackish in the southern part of Laguna Karatá and gradually becoming more saline at the Salonque de Kauropura. Open oceanic salinity does not appear until well past the Barra de Wawa at the river mouth.

Since these brackish coastal lagoons are virtually unexplored biologically, two different localities were selected within the lagoonal system; one along the slightly brackish southern Laguna Karatá near Karatá Village, and one along the more saline Salonque de Kauropura. The shorelines of the lagoons and final river channel are lined with dense thickets of the red mangrove (*Rhizophora mangle*) (Figure 30) and most of the molluscan fauna is mangrove-associated. Open channel and lagoon bottoms are covered with muddy-sand, and oyster bars occur in deeper areas. Characteristic mollusks from the Karatá and Kauropura estuarine localities include:

Gastropods

Neritina piratica Russell, 1940 (Figure 28)
Neritina reclivata (Say, 1822)
Littorina angulifera (Lamarck, 1822)
Littorina nebulosa (Lamarck, 1822)
Cerithidea pliculosa veracruzensis Bequaert, 1942
Melongena melongena (Linnaeus, 1758)
Melampus coffeus (Linnaeus, 1758)

Bivalves

Crassostrea rhizophorae (Guilding, 1828) (Figure 22)
Crassostrea virginica (Gmelin, 1791) (Figures 26, 27)
Polymesoda placans (Hanley, 1845) (Figure 29)

Although faunistically impoverished, the Wawa estuary is probably typical of the Miskito coastal lagoonal system, and shows a degree of endemism. The presence of *Neritina piratica* Russell, 1940, *Cerithidea pliculosa veracruzensis* Bequaert, 1942, and *Polymesoda placans* (Hanley, 1845), all of which are restricted to the western Caribbean, demonstrates the close relationship of the Wawa assemblage with those to the north (Honduras) and to the south (Costa Rica).

Within the final channel of Barra de Wawa, a large, slender variant of *Crassostrea virginica* (Gmelin, 1791) (resembling the Floridian Pleistocene *C.labelleensis* Olsson & Harbison, 1953) forms massive reeflike bars in deeper, more saline water. The large carnivorous gastropods *Thais floridana* (Conrad, 1837) and *Melongena melongena* (Linnaeus, 1758) are common on these bars and are the primary predators of the oysters.

SYSTEMATIC SECTION

The holotypes and paratypes of the following new species are deposited in the type collection of the Division of Mollusks, Section of Invertebrate Zoology, the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. A voucher collection of at least one specimen of each species listed has also been deposited in the main collection of the Carnegie Division of Mollusks.

SYSTEMATICS

Gastropoda
Caenogastropoda
Tonnoidea
Ficidae
Ficus Röding, 1798
Ficus villai new species
(Figures 33, 34, 35)

Description: *Ficus* of average length for genus (adults av. 62 mm), elongated, pyriform, belonging to *Ficus communis* Röding, 1798 species complex. Shell ornamented with thick spiral cords that are better developed than longitudinal cords. Spiral cords colored with irregular, small, pale brown and white dots. Some specimens with broad, dark brown longitudinal flammules, producing "zebra" pattern. Shell thin, lightweight, but structurally strong. Shoulder rounded, gently sloping. Suture depressed, subcanaliculate. Spire elevated above shoulder line, slightly scalariform. Shell surface covered with evenly-spaced, intersecting longitudinal and spiral cords, producing fenestrate patterns. Spiral cords much stronger and better-developed than longitudinal cords, approximately four times as thick (Figure 35). Thinner, fine secondary cord present between each pair of thick primary cords, with secondary cord being approximately as thick as thin longitudinal cords. One or two extremely fine, hairlike, tertiary spiral cords present on either side of secondary spiral cord, giving areas between thick primary cords a silky appearance. Average specimen (based on type lot) with 26 large primary cords on combined body whorl and siphonal canal. General apertural shape elongately ovate, tapering gradually into open siphonal canal. Aperture proportionally wide, approximately equal in size to ventral half of body whorl. Edge of labrum in adult specimens (such as holotype) thickened, reinforced with thin, white, callus-like deposit. Well-preserved specimens show slight undulation along labral edge, with raised areas corresponding to edges of large, primary spiral cords. As typical of all known members of *Ficus communis* species complex, protoconch bulbous, mammillate in appearance, smooth, consisting of 1½ whorls. In fresh specimens, color somewhat variable, generally tan or pale brown with large, wide brown, longitudinal flammules of varying intensities (such as on holotype, Figures 33, 34). On many specimens (such as holotype), primary cords exhibit faint pattern of alternating pale whitish-tan and light brown elongated spots. Depressed subsutural area whitish-tan, paler than rest of body whorl. Anterior half of siphonal canal light brown, darker than body whorl. Protoconch pale whitish-tan. Interior of aperture brown, becoming lighter in color toward labral edge, and with prominent, widely-spaced dark brown stripes that correspond to external primary spiral cords. Columellar side of siphonal canal white. Interior of siphonal canal characteristically dark brown, several shades of intensity darker than aperture interior or body whorl exterior.

Type material: Holotype (CMNH 17339) length 67 mm, width 36 mm; Paratype lot (7 specimens) (CMNH 37340) ranging from length 44 mm, width 27 mm, to length 77 mm, width 44 mm. All type material from the type locality.

Type locality: On beach, high tide line, Barra de Wawa, northern side of Wawa River mouth (Station 3), Miskito Coast, Nicaragua.

Additional localities: Fragmentary specimens were also seen on beach, high tide line, southern side of Wawa River mouth (Station 4), near Wawa Village, Miskito Coast, Nicaragua.

Distribution: At present, collected only from the area of the Wawa River mouth, Miskito Coast, Nicaragua, but may extend from the Honduran Miskito Coast, near Cabo Gracias a Dios, southward to Bluefields, Nicaragua. Discussions with local shrimpers have indicated that *Ficus villai* n.sp. is frequently taken in shrimp nets during shallow (app. 15–20 m depth) trawls off the Cabo Gracias a Dios coast, and that the local fishermen are familiar with this locally-common species. Broken, fragmentary specimens of *Ficus villai* were also collected at Puerto Cabezas (Station 2), but the condition of these was too poor to be part of the type lot.

Etymology: Named for Dr. Jaime Villa, Professor of Biological Sciences, Florida Atlantic University, who assisted me in collecting along the Wawa River area and who was instrumental in securing my involvement in the C.C.C. Miskito Coast research project.

Remarks: As presently understood, the *Ficus communis* complex consists of three shallow water species with disjunct distributions within the tropical and warm-temperate western Atlantic; *Ficus communis* Röding, 1798, (Figures 44, 45) a Carolinian Province, warm-temperate species that ranges from Cape Hatteras, North Carolina to Miami, Florida, and from Naples, Florida around the Gulf of Mexico to Isla Contoy, Yucatán, Mexico, and two tropical, Caribbean Province species, *Ficus villai* n.sp., restricted to Miskitia, and *Ficus lindae* Petuch, 1988 (Figures 40, 41), restricted to northern Colombia and the Gulf of Venezuela area. These distributions are shown in Figure 46.

Of the two previously-described species, *Ficus villai* is most similar, in both shell size and thickness, to the Carolinian *F.communis*. The new species differs from its common and well-known congener in the following ways; *1. shell shape—F. villai* is a more slender shell with a higher, stepped spire; *2. shell sculpture*—the new species has a very distinct sculpture pattern composed of thick, prominent, high-relief, primary spiral cords that dominate the sculpture (Figure 35), while *F. communis* has a much lower-relief pattern composed of weaker primary cords that are nearly equal in size to the secondary cords (Figure 45); *3. shell color—F. villai* is a much darker-colored shell, generally with dark longitudinal flammules (Figure 33) and always with a prominent, dark brown end to the siphonal canal, while *F. communis* is a lighter-colored shell, lacking both the longitudinal, "zebra"-type flammules and the darkly-colored anterior end.

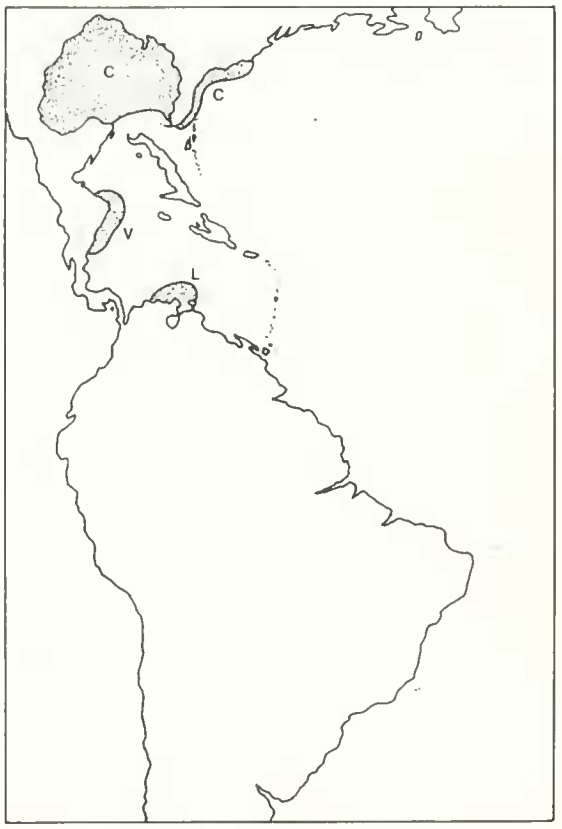


Figure 46. Distributions of the shallow water *Ficus* Röding, 1798 species of the western Atlantic. C = *Ficus communis* Röding, 1798; V = *Ficus villai* new species; L = *Ficus lindae* Petuch, 1988.

The remaining member of the complex, *Ficus lindae* is the least similar to the new species, differing in having a larger and much thinner, almost paperlike, shell. As in the comparison with *F. communis*, *F. villai* also differs from *F. lindae in* three distinct ways; *1. shell shape*—the new species has a proportionally more slender, less inflated shell with a higher, more elevated spire; *2. shell sculpture—F. villai* exhibits a sculpture pattern of dominant, high-relief primary spiral cords with interstitial smaller secondary and tertiary spiral cords, while *F. lindae* (Figure 40) has much reduced, much lower-relief primary spiral cords, a single reduced, secondary spiral cord, and no tertiary cords; *3. shell color*—although both species have similar brown shells with longitudinal darker brown flammules, *F. villai* has a pale, whitish-tan subsutural area and a dark brown siphonal end, both of which are lacking in *F. lindae*.

The new species also shows some morphological similarity to *Ficus carolae* Clench, 1945, a deep water (200 m depth) species from off the Florida Keys and Campeche Banks of Yucatan, Mexico. This bathyal ficid

somewhat resembles *F. villai*, particularly in shell size, shape, and proportions, but differs in having less-developed primary spiral cords and in having a paler-colored shell that is conspicuously and characteristically marked with scattered large, elongated, dark brown spots. *Ficus carolae* may represent a deep water, continental slope-dwelling offshoot of the shallow water *Ficus communis* complex. The two other known deep water western Atlantic ficids, *F. atlantica* Clench & Aguayo, 1940 (900 m depth off central Brazil) and *F. howelli* Clench & Aguayo, 1940 (200–400m depth from Cuba to Trinidad), both have extremely inflated, paper-thin shells, short, stubby siphonal canals, and regularly-arranged, darkly-spotted color patterns. These two species, together, differ greatly from the *F. communis* complex, and appear to represent a separate, distinct, unrelated group.

With the discovery of the Miskitian *Ficus villai*, it is now known that the western Atlantic houses six species of Ficidae. Of these, three live in deep water (200–400 m), continental slope areas and three prefer shallow water, neritic environments. The three shallow water species can be separated as follows (+ = present, − = absent):

	F. villai	*F. communis*	*F. lindae*
1. prominent 1° spiral cord	+	−	−
2. 2° and 3° spiral cords	+	+	−
3. dark longitudinal flammules	+	−	+
4. white spots on spiral cords	+	+	+
5. pale subsutural area	+	−	−
6. dark siphonal end	+	−	−

Cancellarioidea
Cancellariidae
Cancellaria Lamarck, 1799
Cancellaria mediamericana new species
(Figures 31, 32)

Description: Typical western Atlantic *Cancellaria* s.s., of average length for genus (adults av. 35 mm), crudely biconic, with inflated body whorl. Shoulder angled, with flattened subsutural area. Anterior canal short, open. Inner lip along columella with 2 columellar and 1 siphonal folds. Posteriormost columellar fold largest, overlying siphonal fasciole. Body whorl and spire whorls with heavy, coarse cancellate sculpture. Shell thick, structurally strong, reinforced by heavy cancellate sculpture. Outline of body whorl and spire whorls rounded. Edge of shoulder acute, marked with carina-like spiral cord. Flattened subsutural areas give scalariform appearance to spire. Shell surface covered with evenly-spaced, intersecting longitudinal and spiral cords, producing even cancellate sculpture. Cords of equal size and shape. Intersection of cords producing low, rounded bead, giving shell surface pebbly appearance. Holotype with 33 longitudinal cords and 14 spiral cords on body whorl. Aperture proportionally large, broad, semielliptical in shape. Inner edge of labrum with 13 large, thin cords that extend into aperture.

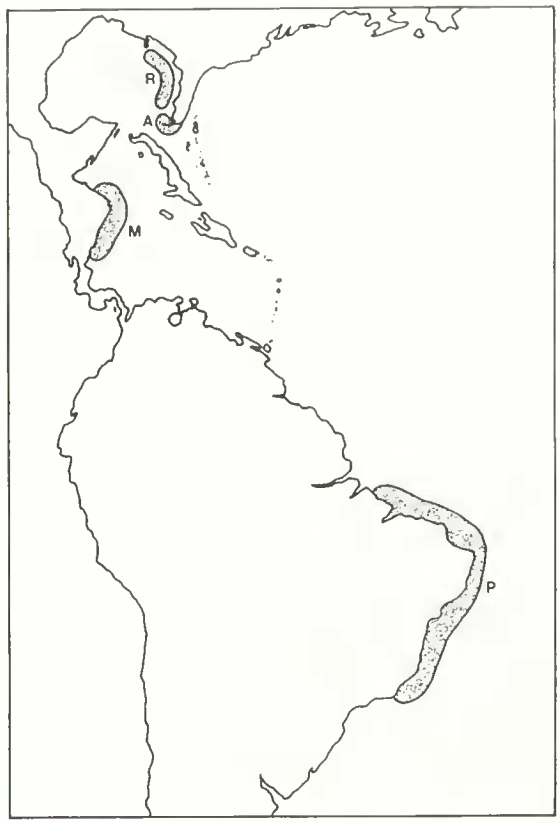


Figure 47. Distributions of the geographically-restricted species of *Cancellaria* Lamarck, 1799 (*sensu stricto*) in the western Atlantic. R= *Cancellaria richardpetiti* Petuch, 1987; A = *Cancellaria adelae* Pilsbry, 1940; M = *Cancellaria mediamericana* n.sp.; P = *Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992. The distribution of the widespread *Cancellaria reticulata* (Linnaeus, 1767) is not shown.

Labral cords disappear in interior of aperture. Entire columellar region overglazed with thin callus. Callus thicker along anterior end, thinning toward posterior end. Both columellar folds and single siphonal fold with single large, flattened keel. Posteriormost and largest fold with very faint, poorly-developed secondary ridge along anterior side. Protoconch paucispiral in form, composed of 2½ low, inflated, glassy whorls. Protoconch of holotype deviated from main shell axis by approximately 15° (Figure 48). Base shell color pale cream-white. Body whorl with 3 wide, evenly-spaced, continuous dark reddish-brown bands, one around anterior end, one just anterior to mid-body, and one around shoulder. Spire whorls with single wide, reddish-brown band. Anterior tip of shell, anterior canal, and siphonal fasciole pale yellow-tan. Protoconch pale cream-white. Columellar and siphonal folds white.

Type material: Holotype, (CMNH 47341) length 34 mm, width 20.5 mm; Paratypes, (CMNH 47342) (2 specimens), length 34 mm, width 20 mm and length 36 mm, width 22 mm. All type material from the type locality.

Type locality: On beach, high tide line, Barra de

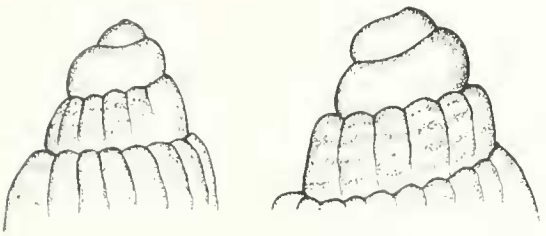


Figure 48. Detail of protoconchs of *Cancellaria* species. (Left) *Cancellaria reticulata* (Linnaeus, 1767), drawn from specimen from Sanibel Is., Florida (Figure 44). (Right) *Cancellaria mediamericana* n.sp., drawn from holotype (Figures 31, 32). Note proportionally larger size and flexure away from shell axis of *C. mediamericana*.

Wawa, northern side of Wawa River mouth (Station 3), Miskito Coast, Nicaragua.

Distribution: At present, known only from the area of the Wawa River mouth, Miskito Coast, Nicaragua, but may extend from the Honduran Miskito Coast, near Cabo Gracias a Dios, southward to Bluefields, Nicaragua. A specimen in the private collection of Mr. Leonard Hill, Miami, Florida, reportedly taken by commercial shrimpers from off Cabo Gracias a Dios, supports a wider range for the new species.

Etymology: "*mediamericana*", "Central American," in reference to the confined range of the new species along the eastern coast of Central America.

Remarks: *Cancellaria mediamericana* n.sp. is the newest member of a characteristic western Atlantic species complex centered around the widespread *Cancellaria (s.s.) reticulata* (Linnaeus, 1767) (Figures 36). That well-known and common species ranges from North Carolina, throughout the Gulf of Mexico, along the Antilles Arc, and southward to northern Brazil. Besides *C. reticulata* and *C. mediamericana*, the complex also includes three other species with restricted geographical ranges (Figure 47). These are: *Cancellaria richardpetiti* Petuch, 1987 (100–200m depth off western Florida), *Cancellaria adelae* Pilsbry, 1940 (carbonate sand areas, 1–10 m depth, Florida Keys), and *Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992 (central and southern Brazil) (Figure 37). Of the members of the complex, *C. mediamericana* is most similar to the widespread *C. reticulata*, but differs in the following ways; *1. shell shape*—the new species has a more inflated shell with a wider aperture; 2. *columella*—*C. mediamericana* has only two columellar folds, with the large posteriormost fold being flattened and keel-like, while *C. reticulata* has three folds with the large central fold being characteristically bifid in form; 3. *protoconch*—the protoconch of the new species is proportionally large, inflated, and bulbous with a slight flexure away from the main shell axis, while that of *C. reticulata* is proportionally much smaller (Figure 48), tightly cylindrical in form, composed of three whorls, and is aligned with the main shell axis; *4. color*—in the new species, the shell is marked with three solid color bands, while in *C. reticulata*, the color bands are discontinuous, broken into a series of separate, large, rectangular maculations.

Cancellaria mediamericana is also similar to the Brazilian *C. petuchi* Harasewych, Petit & Verhecken, 1992 (Figure 37) but differs in the following ways; *1. shell shape*—although both species have widely inflated body whorls, *C. mediamericana* has a sharply-angled shoulder and a flattened, planar subsutural area, while *C.petuchi* has a distinctly rounded shoulder; 2. *shell sculpture*—while *C. mediamericana* has a sharp, strong reticulate sculpture pattern that persists onto the body whorl, *C. petuchi* has a reduced sculpture pattern of low, rounded ribs that become obsolete on the body whorl. Both species, although widely separated geographically, have similar inflated, bulbous protoconchs, triple-banded continuous color pattern, and have only two, flattened, keel-like columellar folds.

The other two species of the complex, *C.adelae* Pilsbry, 1940 and *C. richardpetiti* Petuch, 1987, are both more similar to *C.reticulata* than to *C. mediamericana*. The deep water, bathyal *C.richardpetiti* is a distinctly elongated shell with a high, protracted spire. The Florida Keys endemic *C. adelae*, although generally similar to *C. reticulata*, has reduced shell sculpture, producing a smooth body whorl like that of *C. petuchi*. Both species, *C.richardpetiti* and *C. adelae*, however, have three columellar folds and have bifid, large central folds. In the last character, particularly, these two species much more closely resemble *reticulata* than *C. mediamericana*. For a comparison of the shell morphologies of *C. reticulata*, *C. adelae*, and *C. petuchi*, see Harasewych, Petit & Verhecken (1992). The widespread Caribbean, Miskitian, and Brazilian *Cancellaria* species can be separated as follows (+ = present, − = absent):

	C. mediamericana	*C. reticulata*	*C. petuchi*
1. inflated protoconch	+	−	+
2. solid color bands	+	−	+
3. columellar callus	+	−	+
4. 3 columellar folds	−	+	−
5. 2 columellar folds	−	+	+
6. bifid central fold	−	+	−
7. angled shoulder	+	+	−

Conoidea
Conidae
Conus Linnaeus, 1758
Leptoconus Swainson, 1840
Conus (Leptoconus) paschalli new species
(Figures 2, 3)

Description: *Conus* of smaller-than-average length for subgenus *Leptoconus* (adults av. 24 mm), with stocky body whorl, wide shoulder, and proportionally low spire. Shoulder sharply-angled, subcarinated. Spire whorls flattened, noncanaliculate. Operculum unknown. General shell form subpyriform, with convex sides on body

whorl. Body whorl tapers abruptly anteriorly, pinching-off noticeably to produce narrow siphonal area. Spire whorls slightly raised above suture line, giving stepped appearance to overall spire. Body whorl smooth and polished, marked with numerous very faint longitudinal growth lines. Spire whorls marked with very numerous, closely-spaced crescent-shaped threads. Anterior one-third of body whorl encircled with 9–11 evenly-spaced, deeply-impressed spiral sulci. Aperture proportionally narrow, widening slightly on anterior one-half of shell. Protoconch unknown, missing on holotype and type lot. Based upon proportions of broken early whorls, protoconch probably large and bulbous. Base color white or pale yellowish-white, overlaid with 8–10 evenly-spaced spiral bands of large orange dots and blotches. In some cases, such as in holotype (Figures 2, 3), dots and rectangular blotches coalesce to produce large, widely-spaced orange longitudinal flammules arranged in "zebra" pattern. Clear white band, devoid of markings, except for few small spots, present just anteriorward of midbody line. Clear band separates dots and longitudinal flammules into two wide sections, one extending from shoulder to below midbody line, and a narrower one extending around anterior end of shell. Anterior tip of shell very pale pinkish-lavender. Spire whorls white, marked with widely spaced, orange, crescent-shaped flammules. Early whorls (and presumed protoconch) pale orange. Interior of aperture white. Based on small patch still adhering to outer lip of holotype (later removed by cleaning in sodium hypochlorite), periostracum is thick, heavy, brown in color, marked with very fine, longitudinal striae.

Type material: Holotype, (CMNH 47344) length 26 mm, width 14 mm; Paratypes (7 specimens), (CMNH 47345) ranging from length 20 mm, width 11 mm, to length 27 mm, width 14.5 mm. All type material from the type locality.

Type locality: On beach flat, low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach areas near Bragman's Bluff and Puerto Cabezas, Nicaragua, but may extend southward to Bluefields, Nicaragua.

Etymology: Named for Dr. Norman Paschall of Largo, Florida, who assisted me in collecting in the Bragman's Bluff area.

Remarks: Of the known Caribbean small *Leptoconus* species, *Conus paschalli* is most similar to *Conus portobeloensis* Petuch, 1990 from the San Blas Islands region of Panama. The new species differs from its southern congener in the following ways; *1. shell shape*—*C. paschalli* is a smaller (av. 24 mm) species than *C. portobeloensis*, with a stockier, proportionally shorter, and more pyriform body whorl; the shoulder of *C. paschalli* is sharply-angled, almost carinated, while *C. portobeloensis* has a more rounded shoulder edge with only the faintest hint of a carina; *2. spire*—the spire of of *C. paschalli*, although low like that of *C. portobeloensis*, is distinctly stepped, with the spire whorls being slightly raised above each subsequent suture line; the spire of the Panamanian species has depressed sutures, producing a gradually-sloping spire outline instead of a scalariform one; the spire whorls are planar on the new species, while those of *C. portobeloensis* are sloping and faintly canaliculate; *3. shell sculpture*—*C. paschalli* has a smooth shell with faint longitudinal striae, while the shell of *C. portobeloensis* is distinctly sculptured with fine spiral threads and striae; the anterior third to the body whorl of *C.paschalli* is encircled with 9–11 large, deeply-incised sulci, while the anterior third of *C. portobeloensis* is encircled by at least 20 thin, faint raised cords and an equal number of shallow, thin sulci; *4. color*—while both species have a color pattern composed of spiral lines of dots and large coalescing longitudinal flammules, *C. paschalli* has fewer rows of dots and the individual dots are proportionally larger; the anterior tip of *C. portobeloensis* is pale yellow-orange while that of *C. paschalli* is pale pinkish-lavender. *5. habitat*—judging from the type locality, the new species prefers muddy sand localities in shallow muddy water areas along the river effluent zone of the Miskito Coast of Nicaragua; *Conus portobeloensis*, on the other hand, lives in an offshore (30 m depth) carbonate substrate—clean water environment (see Petuch, 1990:68) off the Colón and San Blas coasts of Panamá. Neither species, nor anything resembling them, has been collected along the intervening clean sandy coast of Costa Rica (Houbrick, 1968), demonstrating geographical and ecological separation.

Bivalvia
Pteriomorpha
Arcoida
Arcidae
Noctia Gray, 1857
Noctia (s.s.) lindae new species
(Figures 9, 10)

Description: Shell small for genus (adults av. 25 mm), equivalve elongated, subtrigonal in shape. Posterior end only slightly expanded, truncated, sharply angled, tapering to sharp point. Angled posterior truncation bordered by large, prominent posterior ridge that runs from umbones to posterior tip. Shallow medial depression present on posterior end above posterior ridge. Umbones placed extremely forward, in anterior one-third of shell. Anterior end not expanded, rounded, without angled ridge. Shell surface with 30–32 evenly-spaced, low, wide, rounded primary radial ribs. Thin, rounded secondary radial rib present between each pair of wide primary ribs. Secondary rib bisected by fine incised line. Primary and secondary radial ribs covered by and intersecting with very fine, closely-packed concentric growth lines, giving ribs slightly roughened appearance. Intermittent

large concentric growth lines present, corresponding to periodic cessations in shell growth. Shell margin and inner margin marked with 30–32 sharp, well-developed crenulations that correspond to thin secondary ribs. Beaks large, prominent, angular, projecting above hinge line. Umbones well-developed, recurved. Beaks and umbones strongly opisthogyrate. Hinge line straight, with coarse taxodont dentition. Posterior teeth larger than anterior teeth. Hinge ligament elongated, broad, with transverse ligamentary grooves at right angles to hinge line. Ligamentary grooves 7–8 in number, placed anteriorly to umbones. Anterior muscle scar proportionally small, oval, at extreme anterior end. Posterior muscle scar proportionally large, oval, formed at base of long, narrow, low flange. Posterior flange extends upward into umbonal interior. Pallial line weakly developed, straight, following edge of shell margin just above marginal crenulations. Shell pale-to-bright lemon-yellow or cream-orange, with posterior end and area above posteroventral angle being darker yellow-orange. Umbones and beaks brightly colored, generally dark reddish-orange or bright cherry red. Shell interior pale yellow or yellowish-white, with some specimens (holotype and 6 paratypes) having darker yellow-orange stain deeper within. Occasional specimens (such as one left valve paratype) with dark red-orange stain that extends from umbonal interior to posterior margin. Periostracum (Partially preserved on two left valve paratypes; removed from holotype pair by soaking in sodium hypochlorite solution) thick, black, coarsely lamellose, marked with thin concentric striae. Periostracum eroded off of beaks of all specimens examined.

Type material: Holotype, (CMNH 47367) length 25.5 mm, width 15 mm; Paratypes, (12 single valves, CMNH 47343), ranging from length 20 mm, width 13 mm to length 29 mm, width 18 mm. All type material from the type locality.

Type locality: On lower beach flat at low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach area near Bragman's Bluff, Puerto Cabezas, Nicaragua, but may possibly be found southward along the Miskito Coast.

Etymology: Named for my wife, Linda Joyce Petuch.

Remarks: *Noetia lindae* is the first member of its genus (s.s.) to be recorded from the Caribbean region, and only the second species of *Noetia* s.s. to be found in the western Atlantic. The other species, *Noetia bisulcata* (Lamarck, 1819) occurs along eastern South America, from Surinam to Uruguay (range and illustration in Rios, 1975: fig. 949). No other *Noetia* s.s. is known to occur in the area between *N. lindae* and *N. bisulcata*. The larger *Noetia ponderosa* (Say, 1822) from the Carolinian Province belongs to (and is the type of) the subgenus *Eoutia* MacNeil, 1938, and represents a different and separate *Noctia* lineage. The Panamic *Noctia reversa* (Sowerby, 1833) and *Noctia olssoni* Sheldon and Maury, 1922 are very similar to *N. lindae*, and the new Caribbean species appears to be intermediate in shell form between its two Pacific relatives; having the more elongated shape of *N. olssoni* and the strong, prominent posterior ridge and high beaks of *N. reversa*.

In general shell shape and size, *Noctia lindae* is most similar to the South American *N. bisulcata*, but differs in the following ways; *1. shell shape—N. lindae* is a much more elongated species with a projecting, distinctly pointed posterior end, while *N. bisulcata* has a more ovate shell shape with a wide, blunt posterior end; the beaks of the new species are located much more anteriorly, within the anterior one-third of the shell, whereas the beaks of *N. bisulcata* are more medially located, almost at the midbody line; the dorsal posterior area immediately above the posterior ridge is flattened in *N. lindae*, while in *N. bisulcata* the posterior dorsal area is raised and laterally flattened; *2. color—N. lindae* is a much more colorful shell than its southern relative, often exhibiting a bright yellow or yellow-orange shell with red umbones, while *N. bisulcata* has a more subdued shell color, being white or pale yellow-white with light orange umbones.

Pterioida
Pectinoidea
Plicatulidae
Plicatula Lamarck, 1801
Plicatula miskito new species
(Figures 16, 17, 18, 9)

Description: Shell small for genus (holotype 13 mm), ovately subtrigonal in shape, flattened, with right valve attached to substrate. Auricles present but poorly-developed, with posterior auricle larger and wider than anterior auricle. Interior porcellaneous. Hinge line straight. Exterior of free (left) valve with very fine, raised concentric lines that become stronger and more lamellose toward shell margin. Area near beaks decorated with 18 very fine beaded radial ribs. Radial ribs flatten and disappear halfway between beak and shell margin. Shell margin faintly crenulate. Beak poorly-developed, almost planar, with small, faint sharply-pointed umbo projecting only slightly above hinge line. Entire hinge structure proportionally large, typically spondyloid, with narrow, small, elongated chrondrophore. Chondrophore pit of upper (left) valve flanked by two crural ridges, each with single, smooth ball-type teeth. Chondrophore pit of bottom (right) valve flanked by two elongated sockets and two small elongated teeth. Single adductor scar posterior to center of shell, almost circular in shape. Pallial line deeply incised, located subcentrally, following shell margin. Exterior of free (left) valve white with numerous fine, radiating, pale reddish-brown lines and large, scattered, dark reddish-brown spots. Shell margin marked with large, prominent, equally-spaced, dark reddish-

brown streaks. Subumbonal area stained pale tan. Umbo reddish-tan. Attached (right) valve pure white. Interior of left valve white with large pale tan stain, extending from adductor scar to umbonal area. Margin of shell interior of left valve marked with prominent, equally-spaced dark reddish-brown streaks, corresponding to those seen on shell exterior. Ball-and-socket teeth of both valves pale tan.

Type material: Holotype (pair) (CMNH 47366) length 13 mm, width 5 mm.

Type locality: On lower beach flat at low tide, in shell rubble bed, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua. Holotype found attached to interior of *Noctia lindae* n.sp. valve (Figures 18, 19).

Distribution: At present known only from shell rubble beds at Bragman's Bluff, Puerto Cabezas, Nicaragua.

Etymology: Named for the Miskito Indians, as a noun in apposition.

Remarks: *Plicatula miskito* n.sp. is only the second-known representative of its genus in the western Atlantic, and is the first *Plicatula* to be collected on the Miskito Coast. The other Atlantic member, *Plicatula gibbosa* Lamarck, 1801, which ranges from North Carolina to Brazil, is an abundant but very different-appearing species and does not seem to be closely related. *Plicatula miskito* differs from its widespread and well-known congener in the following ways; *1. size—P. gibbosa* is a much larger species, averaging 25 mm in length (Abbott, 1974: 450), while *P. miskito* is a much smaller animal, with the holotype being only 13 mm in length; *2. shape and sculpture*—the common *P.gibbosa* is a very rugosely-sculptured species with 5–7 prominent, high, raised plications that give the shell a strongly ribbed appearance (hence the common name, the "kitten's paw"), while the shell of *P. miskito* lacks the raised plicae having, instead, fine beaded radial riblets near the umbo; the shell margin and commissure of *P. miskito* are relatively straight and flattened while those of *P. gibbosa* are strongly undulate.

Morphologically, the new species is most similar to *Plicatula penicillata* Carpenter, 1857 from the Panamic Province, and its presence in the Miskitian malacofauna further underscores the Pacific faunal affinities of the Nicaraguan Caribbean coastal region. The two species are strikingly similar, particularly in size, shape, and color pattern. Both species exhibit the distinctive and characteristic large dark streaks along the shell margin and both have the large tan stain within the shell interior. *Plicatula miskito* differs from *P. penicillata* primarily in the surface sculpture of the free valve; while the new species is relatively smooth, with only faint concentric laminae and radial riblets, its Panamic congener has a more crenulate, rougher, surface, often decorated with small ribs and spines. Otherwise, the two species are extremely close and they form an impressive example of a previously-unknown Panamic-Caribbean sibling species pair.

Heterodonta
Veneroida
Mactroidea
Mactridae
Mactra Linnaeus, 1767
Mactra inceri new species
(Figures 7, 8, 11)

Description: Shell typically mactrid in form, thin, fragile, with convex, inflated valves, of average size for genus. Shell shape generally oval-subtrigonal, with high, pointed umbones and slightly concave posterior-dorsal area. Faint, low, rounded keel borders posterior-dorsal area and posterior margin of umbones. Posterior end slightly pointed, anterior end rounded. Beaks placed slightly anterior to shell midline (based on total shell length). Lunular region wide, deeply impressed. Entire shell exterior covered with very fine, closely-packed concentric growth lines, giving shell silky texture. Growth lines become coarser toward shell margin. Beaks large, prominent, trigonal in shape, projecting above hinge line. Umbones highly recurved, strongly prosogyrate. Resilifer proportionally large, trigonal in shape, with apex of triangle bent anteriorally. Resilifer set in large, cup-shaped chondrophone that overhangs umbonal region, producing deep subumbonal cavity. Edges of resilifer-chondrophore complex bounded by thin, raised, slightly concave shelly lamina. Cardinal teeth prominent, with posterior flange overhanging resilifer. Lateral teeth thin, elongated, bladelike, with anterior lateral tooth having projecting, trigonal flange. Anterior adductor scar near extreme anterior margin of shell, thin, elongated in shape. Posterior scar nearly circular in shape, located near extreme posterior shell margin. Pallial line prominent, sinusoidal in form, with long, deep, sublinguiform pallial sinus. Pallial sinus extends horizontally well past shell midline (see Figs. 8, 11). Shell exterior and interior uniform pale cream-white. Periostracum (Present only as fragmentary remnants along margin of holotype valve) pale yellow-tan, thin, translucent, with silky texture.

Type material: Holotype, (single right valve) (CMNH 47338), length 35.5 m, width 41 mm; Figured paratype, (single right valve, CMNH 47346), length 24 mm, width 27 mm; Paratypes, (3 single valves, CMNH 47350), ranging from length 25 mm, width 28 mm to length 33 mm, width 36 mm. All type material from the type locality.

Type locality: On lower beach flat at low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach area near Bragman's Bluff, Puerto Cabezas, Nicaragua, but may possibly be found southward along the entire Miskito Coast.

Etymology: Named for Dr. Jaime Incer, director of IRENA, Managua, Nicaragua, in thanks for his assistance and support of my research while I worked along the Miskito Coast.

Remarks: *Mactra inceri* is the first species of *Mactra* (s.s.) to be reported from the Caribbean Basin. The only other known western Atlantic member of the genus is *Mactra iheringi* (Dall, 1897), which ranges from Venezuela (Weisbord, 1964:381–382) southward to Santa Catarina, Brazil (Rios, 1975:236) and, prior to the discovery of the Miskitian species, the genus *Mactra* (s.s.) was conspicuously absent from northern South America, eastern Central America, and the West Indian Arc. Interestingly enough, the subgenus *Mactrotoma* (typified by *Mactra fragilis* Gmelin, 1791), which is the common Caribbean representative of the Mactridae, was not collected along the Miskito Coast but was replaced by the nominate genus.

Although similar to the South American-Brazilian *Mactra iheringi*, *M. inceri* can be readily distinguished by the following characters; *1. shell shape*—The new species has a less-elongated, more rounded and truncated anterior and; because of this truncated appearance, the umbones of *M. inceri* are located slightly anterior to the midbody line, while those of *M. iheringi* are almost exactly centrally located, directly on the midbody; *2. form of the lunule*—in *M. inceri*, the lunule is distinctly depressed, producing a noticeable concavity along the anterior-dorsal area immediately anterior to the umbones; in *M.iheringi*, the lunular area is simply flattened, producing a straight, sloping surface; *3. pallial sinus*—in *M. iheringi*, the sublinguiform pallial sinus extends horizontally to, or a little beyond, the midbody line (Dall, 1897; Weisbord, 1964:381), while in *M. inceri*, the pallial sinus extends well beyond the midbody line (Figures 8, 11) occupying fully two-thirds of the shell interior; this enlarged pallial sinus demonstrates that *M. inceri* has longer siphons than does its southern congener and lives more deeply buried in the substrate.

Micromactra Dall, 1894
Micromactra miskito new species
(Figures 12, 13)

Description: Shell of average size for genus (av. 27 mm), elongated, thin, fragile, with beaks centrally located. Anterior dorsal margin of shell, immediately anterior to beaks, nearly straight, with only slightest hint of concavity. Anterior end rounded, posterior end pointed but angularly truncated. Low but sharp angular ridge present along entire posterior dorsal edge of both valves. Beaks and umbonal area of shell exterior characteristically sculpted with 6–15 large, prominent, undulating waves. Surface of exterior smooth, shiny, covered with very fine, closely-packed concentric growth lines, giving shell faintly silky appearance. Large umbonal undulations also covered by fine concentric growth lines. Very fine, thin, evenly-spaced radial lines present on anterior one-half of shell. Beaks large, prominent, projecting well above hinge line, roughly trigonal in shape. Umbones highly recurved, strongly prosogyrate. Resilifer trigonal in shape, with apex tipped anteriorly, set in small cup-shaped chondrophone. Cardinal teeth distinctly "V"-shaped. Lateral teeth elongated, bladelike. Anterior adductor scar near extreme anterior margin of shell, oval in shape. Posterior scar of approximately equal size and shape, located near extreme posterior shell margin. Pallial line sinusoidal in form, with short, rounded, wide, pallial sinus. Pallial sinus extends horizontally only about one-third of shell interior. Shell exterior and interior uniform translucent white. Periostracum thin, smooth and silky, adherent, pale straw colored, generally missing on umbones.

Type material: Holotype, (single right valve) (CMNII 47364), length 30 mm, width 19 mm; Paratypes, (5 single valves, CMNII 47352), ranging from length 25 mm, width 17 mm to length 28 mm, width 19 mm. All type material from the type locality.

Type locality: On lower beach flat at low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach area near Bragman's Bluff, Puerto Cabezas, Nicaragua, but may possibly be found southward along the entire Miskito Coast.

Etymology: Named for the Miskito Indians.

Remarks: The finding of a Caribbean *Micromactra* species was one of the most interesting and important discoveries to be uncovered during my research in Nicaragua. Until now, the genus was known from the western Atlantic by only a single cooler-water species, the Brazilian Province *Micromactra jancirocusis* (E.A. Smith, 1915), which ranges from Espirito Santo State, Brazil to Urugnay (Rios, 1975:236). On the other hand, the genus is well-represented in the Eastern Pacific, with at least five species occurring in the Panamic Province alone (Keen, 1971:204).

Of the known *Micromactra* species, both Eastern Pacific and western Atlantic, *M. miskito* most closely resembles the Pacific *M. californica* (Conrad, 1837) which ranges from the Puget Sound southward to Costa Rica, and they form another example of a previously-unknown Panamic-Caribbean sibling species pair. The new species differs from its Pacific analogue in being slightly more elongated with a noticeably more truncated posterior end, in having more prominent, more highly elevated umbones, and in having a slightly more concave lunular area. Otherwise, the two species are very similar, especially in having virtually identical patterns of umbonal undulations.

From the only other Atlantic *Micromactra* species, *M. jancirocusis*, *M. miskito* can be separated by the following characters; *1. shell shape*—the new species has a

much more elongated, slender shell than does *M. janeiroensis,* and the posterior end of *M. lindae* is much more pointed and sharply-angled than the blunted, more rounded posterior of its southern congener; 2. *undulating sculpture*—the undulating, wavy sculpture pattern (the main characteristic of the genus *Micromactra*) is confined to the umbonal region of *M. miskito,* while on *M. janeiroensis* it extends onto the main shell body, often covering as much as two-thirds of the shell surface.

Petricolidae
Petricolinae
Petricola Lamarck, 1801
Petricolaria Stoliczka, 1870
Petricola (Petricolaria) donnae new species
(Figures 24, 25)

Description: Shell thin, fragile, small for subgenus (holotype length 28 mm), elongated, subcylindrical in shape, with dorsal and ventral margins roughly parallel. Umbones rounded, elevated above hinge line, placed far forward near anterior end. Small flattened lunule present just anterior to umbones. Anterior end pointed, posterior end wider and distinctly rounded. Shell exterior covered with numerous fine, closely-spaced radial ribs. Radial ribs, especially those on anterior one-fourth of shell, become coarser and farther apart toward anterior end of shell. Radial ribs crossed by numerous, evenly-spaced concentric ribs. Intersections of concentric ribs with large anterior radial ribs producing small spine-like scales on radial ribs. Umbones rounded, recurved, strongly prosogyrate. Hinge line straight, smooth. Hinge without lateral teeth. Cardinal teeth paired, typically petricolid, with anterior tooth curved and hooklike, and with posterior tooth flattened and bifurcated. Pallial line sinusoidal in form, with long, deep, pointed sublinguiform pallial sinus. Pallial sinus extends horizontally to shell midline. Shell exterior and interior pale cream-yellow, with posterior end stained pale orange. Pale orange color may be staining from the red clay within which the animal had bored, and not part of the actual shell color.

Type material: Holotype (pair) (CMNH 47373), length 28 mm, width 9 mm.

Type locality: On beach near clay cliffs, approximately 1 km north of main pier of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the clay cliff and clay reef areas near Puerto Cabezas, Nicaragua.

Etymology: Named for Mrs. Donna Villa, of Wellington, Florida. Her husband, Dr. Jaime Villa, collected the unique holotype and wished to have the species named for her.

Remarks: Prior to the discovery of *Petricola (Petricolaria) donnae,* the subgenus was known in the western Atlantic from only a single wide-ranging species, *P. (Petricolaria) pholadiformis* (Lamarck, 1818) (Figure 23). Although only a single specimen of the new species has been collected, the new *Petricolaria* is so different that there can be no doubt that it represents a previously-unknown and undescribed animal. The apparent rarity of the new species is most probably an artifact of collectibility. Judging from the abundance of bivalve borings in the clay reefs, the species is probably common, but is deeply buried below the surface and is virtually inaccessible. Rarely, specimens such as the holotype may wash out of broken clay blocks during storms.

The new species can be readily separated from its only western Atlantic congener in the following ways; *1. shell shape—Petricola donnae* is a much shorter, stockier species with a proportionally wider, less elongated shell; the posterior end of *P. donnae* is much wider and noticeably more rounded than the more pointed posterior end of *P. pholadiformis*; the umbones of *P. donnae* are also proportionally narrower and more acute than those of *P. pholadiformis,* and project farther above the hinge line; 2. *shell sculpture*—the posterior and central radial ribs of *P. donnae* are much more numerous and better-defined than those of *P. pholadiformis,* while the anterior radial ribs of *P. donnae* are not as large nor as heavily sculptured as those of *P. pholadiformis* (readily seen in a comparison of Figures 23 and 24).

Of the known American *Petricolaria* species, *P. donnae* is actually most similar morphologically to the Panamic Province *P. cognata* C.B. Adams, 1852, especially in overall shell shape and size. The Pacific *P. cognata,* however, has much coarser and more heavily-sculptured anterior radial ribs, much in the manner of *P. pholadiformis.* Even with this sculptural difference, *P. donnae* is still very similar to *P. cognata* and can be considered to be its Atlantic analogue, just as the Panamic *P. parallela* Pilsbry and Lowe, 1932 is the Pacific analogue of the Atlantic *P. pholadiformis.* Interestingly enough, the normally-common Caribbean clay-dwelling *P. pholadiformis* has not been reported from the Miskito Coast, where it appears to have been replaced by *P. donnae.*

BIOGEOGRAPHICAL IMPLICATIONS

Based upon the faunal evidence presented in this paper and in previous studies (Fluck, 1905–1906; Petuch, 1981,1987,1988), it is now known that the shoreline and estuarine areas of eastern Central America, from approximately Cabo Camaron, Honduras to near Bluefields, Nicaragua, house a combined molluscan fauna that bears only a partial relationship to the surrounding Caribbean Molluscan Province. Since this new faunal subdivision of the Caribbean Province is centered on the Miskito Coast of Honduras and Nicaragua, I here propose the name "Miskitia" for this newly-discovered biogeographical unit. At present, the biogeographical subdivisions of the Caribbean Province, particularly at the subprovincial level, are still virtually unknown, so I prefer to use "Miskitia" as an informal designation—simply to emphasize the atypical Caribbean nature of the nearshore molluscan fauna. As the area is better studied, it

may be proven that Miskitia actually represents a separate and discrete molluscan subprovince.

As presently understood, the tropical Americas contain two types of marine molluscan faunas; a "Caribbean"-type fauna and a "Panamic"-type fauna. A classic Caribbean fauna contains index genera such as *Lithopoma, Puperita, Smaragdia, Cenchritis, Chicoreus, Fasciolaria,* s.s., *Dolicholatirus, Conella, Cariboliva, Turbinella, Cordilyria, Lindapecten* ("*Acquipecten*" *muscosus* complex), *Spengleria,* and in some areas *Voluta* and *Siphocypraea.* A classic Panamic fauna, on the other hand, contains index genera such as *Ancistromesus, Trochita, Jenneria, Malea, Pseudozonaria, Muricanthus, Northia, Agaronia, Noetia* (s.s.), and *Micromactra.* These faunal characterizations were based on assessments of transisthmian assemblages (Caribbean and Eastern Pacific) and were reported on by Olsson (1972), Petuch (1982), Radwin (1969), Vermeij and Petuch (1986), and Woodring (1966). From the results of these studies, it was generally accepted that the Caribbean and Panamic molluscan faunas, with the exception of some analogue species ("cognates" of Radwin, 1969), were quite different-appearing, and that the Panamic fauna was much more diverse and species-rich (Olsson *in* Olsson & Petit,1964: 525). Subsequent works (Petuch, 1987;1988;1990), however, have shown that the Caribbean area, particularly northern South America and isolated islands, does harbor some previously-unrecognized "Panamic" ("paciphiles" of Woodring, 1973) genera such as *Cotonopsis, Truncaria, Agaronia, Aphera, Knefastia,* and *Cyclothyca,* as well as supposedly-extinct genera such as *Falsilyria, Conomitra, Plcioptygma, Cerithioclava,* and *Paraborsonia.* The Caribbean, then, can be seen to be far richer and more complicated, faunistically, than was previously thought.

With the present discovery of the new western Caribbean fauna reported here, the tropical Americas are now known to contain three "Panamic"-type faunas; an Atlantic component containing the Brazilian Province (as defined by Petuch, 1988:166; Harasewych, Petit & Verhecken, 1992) and the Miskitian area of the Caribbean Province, and a Pacific component containing the classic Panamic Province and offshore Cocos Island and Galapagos Islands "Subprovinces" (possibly full provinces). The biogeographical divisions that contain "Panamic"—type faunas and that show close faunal affinities to each other are shown in Figure 49, and as can be seen, Miskitia represents a shallow water Panamic fauna that has been left behind in the western Atlantic after the final closure of the Central American Isthmus in the late Pliocene. A short listing of shallow water and estuarine endemics and their living Panamic analogues (cognates) demonstrates the Panamic-Eastern Pacific nature of the Miskitian fauna:

Miskitia Restricted	**Panamic (Pacific)**
Strombus pugilis nicaraguensis	*S. gracilior*
Ficus villai	*F. ventricosa*
Agaronia hilli	*A. propatula*
Cancellaria mediamericana	*C. obesa*
Conus paschalli	*C. regularis*
Noetia lindae	*N. olssoni*
Pacipecten leucophaeus	*P. tumbezensis*
Plicatula miskito	*P. penicillata*
Micromactra miskito	*M. californica*
Polymesoda placans	*P. nicaraguana*
Petricola donnae	*P. cognata*

Figure 49. Molluscan biogeographical areas of the tropical Americas that show close faunal affinities, particularly in their shoreline assemblages. P = Panamic Molluscan Province; M = Miskitia (subprovince of the Caribbean Molluscan Province ?); B = Brazilian Molluscan Province. All three share genera such as *Agaronia, Noetia* (s.s.), and *Micromactra.* With the Panamic Province, Miskitia also shares species of the *Plicatula penicillata* complex, *Pacipecten,* and the *Petricola* (*Petricolaria*) *cognata* complex.

A close relationship to the other Atlantic "Panamic" fauna, the Brazilian Province, is also readily demonstrated by the following Miskitian endemics and their Brazilian analogues:

Miskitia Restricted	**Brazilian**
Strombus pugilis nicaraguensis	*S. pugilis worki*
Agaronia hilli	*A. travassosi*
Cancellaria mediamericana	*C. petuchi*
Conus paschalli	*C. tostesi*
Noetia lindae	*N. bisulcata*
Mactra inceri	*M. iheringi*
Micromactra miskito	*M. janeirocnsis*

All three "Panamic" faunas can be seen to share the genera *Agaronia, Noetia* (s.s.), and *Micromactra.* Interestingly enough, all three areas also have their own member of a *Strombus* (s.s.) species complex (*S. pugilis nicaraguensis* Fluck, 1905, *S. pugilis worki* Petuch,

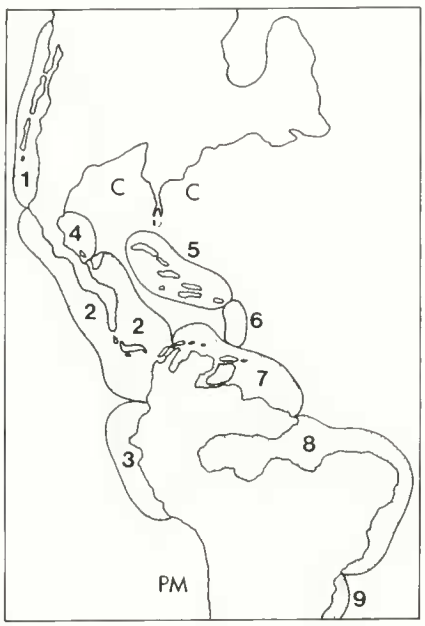


Figure 50. Configurations of the American tropical seas during the early Piacenzian Pliocene, showing the distributions of the subprovinces of the Gatunian Molluscan Province (shaded areas) (taken from Petuch, 1988). 1 = Imperialian Subprovince, 2 = Limonian Subprovince, 3 = Esmeraldan Subprovince, 4 = Agueguexitean Subprovince, 5 = Guraban Subprovince, 6 = Carriacouan Subprovince, 7 = Puntagavilanian Subprovince, 8 = Piraban Subprovince, 9 = Camachoan Subprovince. C = region of the Caloosahatchian Molluscan Province (with four subprovinces; see Petuch, 1997); PM = region of the Protomagellanic Molluscan Province.

1993, and *S. gracilior* Sowerby, 1825), a *Cancellaria* (s.s.) species complex (*C. mediamericana* n.sp., *C. petuchi* Harasewych, Petit & Verhecken, 1992, and *C. obesa* Sowerby, 1832), and *Conus* (*Leptoconus*) species complex (*C. paschalli* n.sp., *C. tostesi* Petuch, 1986, and *C. regularis* Sowerby, 1833).

The shared genera and species complexes of the geographically-separated Panamic and Brazilian Provinces and Miskitia reflect a common origin in the Gatunian Province (Petuch, 1982) (Figure 50) during the late Pliocene, prior to the formation of the Panamanian Isthmus and Amazon River barriers. Since the final closing of Panama (Whitmore & Stewart, 1965:185), the Panamic Province has retained a nearly intact Gatunian appearance (Vermeij & Petuch, 1986) while the Caribbean Province has become a mixture of Gatunian survivors and immigrants from the northern Caloosahatchian Province (Petuch, 1988:115–116; 1997). Prior to the discovery of Miskitia, the only Atlantic area that retained any semblance of the Gatunian Province (Piraban Subprovince) was the Brazilian Province, which shares with the post-closure Panamic Province additional genera such as *Malea*, *Northia*, and *Pleuroploca* (s.s.). Miskitia, then, represents yet another pocket of shallow water Gatunian survivors within the western Atlantic, and one that is contiguous with typical Caribbean assemblages to the north and south.

The ancestral fauna of Miskitia is found within the fossil beds of the Limonian Subprovince of the Gatunian Province (Figure 50), a Pliocene biogeographical area that spanned both sides of the then-open Central American Isthmus. A survey of the eastern Costa Rican Limón and Gatun Formations and western Costa Rican Armuelles and Charco Azul Formations (listed by Olsson, 1922; 1942), which all contain typical Limonian Gatunian elements, will readily demonstrate the Gatunian ancestry of the Recent Miskitian fauna. As in the cases of the Recent Brazilian and Panamic Provinces, Miskitia also contains analogues with the older Limonian Subprovince. These include:

Miskitian Restricted	**Limonian**
Strombus pugilis nicaraguensis	*S. pugiloides*
Ficus villai	*F. carbasea*
Agaronia hilli	*A. costaricensis*
Cancellaria mediamericana	*C. barretti*
Conus paschalli	*C. costaricensis*
Noctia lindae	*N. subreversa*
Pacipecten leucophaeus	*P. costaricensis*
Micromactra miskito	*M.* sp. (Armuelles Form., Olsson, 1942)

These Limonian paleoanalogues appear to be the direct ancestors of the Miskitian species.

The survival of a "Panamic", Gatunian-derived Miskitian fauna in the Caribbean region is also probably due to the retention of a Panamic-type coastal habitat within the western Atlantic. Both the Pacific and Atlantic coasts of Honduras and Nicaragua are typified by siliciclastic, muddy, terrigenous run-off, high productivity environments and both coasts have large mangrove forests with extensive estuarine areas. Although this type of coastline is typical of the Panamic Province south of Mexico, it occurs only sporadically within the Caribbean Basin, where carbonate environments predominate. To the north of Miskitia, the extensive coral reef systems of the Great Barrier Reef of Belize and the Bay Islands of Honduras predominate. To the south, the open, clean sand coasts and coral reef systems of Costa Rica, Panama, and the San Blas Islands (the Blasian Subregion of Petuch, 1990) represent a mirror image of the carbonate environments of the Bay Islands. The Miskitian area, environmentally and sedimentologically, represents an "island" of muddy nearshore habitats wedged between these two extensive coral-dominated subregions. This siliciclastic-dominated environment may have been present since before the closure of Panama, allowing the older Gatunian elements to survive within the Caribbean Sea even though their congeners died-out in the other Atlantic Gatunian subprovinces due to lowered productivity and increased carbonate build-up (Vermeij & Petuch, 1986).

The discovery of Miskitia further underscores the faunal and temporal heterogeneity of the Caribbean Molluscan Province and, hopefully, will focus the attention

of biogeographers on one of the most biotically complicated, but yet unexplored, areas of the entire Atlantic Ocean.

ACKNOWLEDGMENTS

For assistance in the collection of specimens from the Wawa River and Puerto Cabezas areas, I thank Dr. Jaime D. Villa, Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida, Dr. Norman Paschall, Largo, Florida, and Sr. Raimundo Solórzano, Managua, Nicaragua. I also thank the Caribbean Conservation Corporation (CCC), Gainesville, Florida, and Dr. Charles S. Luthin, Director of Programs (CCC), for financial support and for sponsoring this research. Special thanks go to IRENA, Managua, Nicaragua, and its director, Dr. Jaime Incer, for technical, logistical, and financial support while in the field. For patiently typing the manuscript, I thank Mrs. Cynthia Mischler, Department of Geology, Florida Atlantic University.

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